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THE PHYLOGENETIC ORIGIN AND THE NATURE  
OF THE WINGS OF INSECTS ACCORDING  
TO THE PARANOTAL THEORY.<sup>1</sup>

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Within the past century, various and conflicting theories concerning the origin of the wings of insects have been proposed. In order to choose one of these as a "working basis" for further investigation, it is necessary to subject them all to a critical examination, in order to determine which of them is in accord with the greatest number of known facts, or is the least open to objection—and is therefore the most probable and acceptable. It is with this in view that the different theories, together with the available evidence upon the subject, have been brought together in the following discussion.

The theories dealing with the origin of wings in insects, may be grouped into two classes, one of them containing those theories in which it is maintained that the wings are entirely new structures (or organs "*sui generis*"), while the other group contains those theories in which it is maintained that the wings were evolved from preëxisting structures. As an example of the first type, may be mentioned the views of Kirby, who compares the wings of insects to the lateral expansions of the flanks, strengthened by the ribs and used as gliding planes, in the flying lizard *Draco*. Kirby appears to regard the wings

<sup>1</sup> Contribution from the Entomological Laboratory of the Massachusetts Agricultural College, Amherst, Mass.

of insects as new structures, although he is not so outspoken in the matter as Audouin (1824) and Lacordaire (1834), who regard insects' wings as organs "*sui generis*." Lacordaire in particular, seems to regard further discussion of the subject as unprofitable, in view of the fact that, since the wings are (as he thinks) entirely new organs, they can have no relation to any previously existing structures.

It is possible that Audouin and Lacordaire are correct in their contention that the wings are organs "*sui generis*," although they were doubtless influenced in their belief by the then prevalent idea of "special creation," whose adherents maintained that each species (and hence the organs peculiar to it) was created quite independently of other organisms, and consequently the idea of structures arising as modifications of preëxisting structures, was precluded by the very nature of the hypothesis. In accordance with the modern conception of the method and factors of evolution, however, it is difficult to conceive how wings of sufficient size and development to be of any use to the organism could have arisen, save through the predominance of some new function, or use, in organs which had some prior function or significance.

It is not always necessary, however, to suppose that the preëxisting structures originally served any useful purpose, since an *inherent* tendency toward the greater development of certain structures (projections of the body-wall, etc.) might find opportunity for fuller expression, so long as such a development did not lead to a condition detrimental to the organism—in which case natural selection would operate to prohibit further progress along this line, while the persistence of such structures would be assured, if they reached a stage wherein they were capable of furnishing their possessors with a means of successfully coping with their competitors or enemies, or would be of assistance in maintaining the life of the organism. The latter view would seem to be more in accord with our present knowledge of the method of evolution, and is therefore more acceptable than the view that the wings are organs "*sui generis*."

The theories contained in the second group (in which it is maintained the wings have developed from preëxisting structures) are of several types. Thus, the adherents of one theory would derive the wings of insects from the "elytron"-like appendages, or the gills, of Annelidan ancestors; others regard the wings as modified legs, or

other appendages; while others regard the wings as modified respiratory organs (gills or spiracles); and still others think that the wings have developed from the lateral expansions of the tergal region (not necessarily concerned with respiration) which occur in numerous Arthropods. These theories may be briefly reviewed as follows.

Among those who maintain that the wings of insects arose from some preëxisting structures, may be cited the views of Rathke (1834) who compares the foliaceous appendages which appear in the posterior region of the cephalic lobes of the embryo of the Crustacean *Asellus aquaticus*, to a first transient indication of the wings of insects (*teste* Plateau, 1871); and Carus (1839) likewise accepts this view—although he also maintains that the wings have developed from respiratory organs. Dohrn (1881) refers both wings and tracheal gills to the “elytra” of the Annelidan ancestors of insects, apparently influenced by the suggestion of Owen (1848–1855) who regards the wings of insects as metamorphosed tergal branchiæ of the Annelidan ancestors of insects.

The theories dealing with the derivation of the wings from the branchiæ of worms, will be taken up under the discussion of the origin of wings from respiratory organs. It may be remarked, however, that those theories in which it is sought to derive the wings from the gills of worms (or from the parapodial and other structures of the Annelids) take a great deal for granted; and until we have a wider knowledge of more intermediate forms, and their development, any attempts to trace the wings, or any other Insectan structures, to organs which are supposed to be their forerunners in the Annelids, must be regarded as speculative in the extreme.

Latreille (1820) compares the wings to legs; MacLeay considers the wings as greatly modified limbs; Leukart (1848) thinks that wings are repetitions of the legs on the dorsal surface of the body; and Carus and Gerstaecker (1863) regard the wings as limbs arising from the back.

Jaworowski (1896–1897) derives the wings and legs from a common origin, and states that both arise as a simple hypodermal outgrowth within a peripodial depression corresponding to the “lung-like” structure from which he derives the limbs of all Arthropods; the limbs, according to him, being to all intents and purposes, modified protruding respiratory lamellæ. Jaworowski’s theory would thus

come under the discussion of the origin of wings from respiratory structures, but has been taken up at this point, since he brings out certain features having a bearing upon those theories in which it is maintained that the wings are, to all intents and purposes, modified legs.

On page 183, Jaworowski, 1897, mentions that legs and wings can be substituted for one another, in certain insect monstrosities, and cites the description by Nelson, 1889, of a *Zygana* in which a wing had grown in the place of a leg, and also cites the case of an East Indian fig-insect (described by Simroth, 1891) which has segmented appendages instead of wings (see also Fig. 11 of wing of *Zopherus*, by Brues, 1903). I have also observed that in certain Diptera, the halteres may appear to be composed of three segments, but I do not think that the apparently segmented condition of such highly modified structures can be interpreted as the retention of a primitive condition, although I would not utterly deny this possibility; and, since those insects in which the wings arise as hypodermal evaginations within a peripodial cavity are highly specialized forms, I am rather inclined to regard this also as a secondary modification, rather than as a retention of a primitive condition.

Jaworowski (1896) although at first inclined to accept the view that the wings are modified tracheal gills, finally repudiated this view, upon having his attention called by Heider, to Heymons's investigations which demonstrated that in *Sialis* and *Ephemera*, the gill appendages are not homodynamous with the wings, thus disproving Gegenbauer's contention that wings are developed from tracheal gills.

From the preceding discussions, it is evident that the foregoing theories may also imply or expressly include the idea of the derivation of the wings from respiratory structures, in addition to the central idea of the theory; so that it is impossible to divide these theories into sharply defined classes, since they merge into each other through having several ideas in common. The discussion of these theories, therefore, leads up to that of the theories in which it is maintained that wings are modified respiratory organs.

Among those who maintain that the wings are to be derived from organs having a previous respiratory function, may be mentioned the views of Plateau, 1871. Plateau's theory differs from those in which it is maintained that the wings had a respiratory origin, in that he regards the wings as highly modified spiracles.

In support of his contention, Plateau (1871) cites a number of observations, which are, unfortunately, incorrect; and, since his premises are unsound, his conclusions are naturally false also. Thus, he points out that Blanchard (1868), quoting De Blainville, states that no respiratory orifice, or spiracle, is ever found in either the mesothorax or metathorax, and concludes that this absence of respiratory orifices in the segments which bear, or should bear, the wings, gives weight to the hypothesis (long prevalent even in Blanchard's day) that the wings are largely composed of outgrowing tracheæ which have become imprisoned between two integumental lamellæ—a theory accepted by Girard, and many others.

As a matter of fact, the mesothorax and metathorax (*i. e.*, the wing-bearing segments) are usually the only thoracic segments supplied with spiracles, which were either overlooked by the earlier investigators, or were ascribed to the wrong segment, due to the fact that it was not then known that the thoracic spiracles might migrate (during ontogenetic development) from the segment in which they were formed during embryological development, and, taking up a position in the intersegmental region, appear to belong to the segment in front rather than to the segment behind them.

Plateau goes on to say that it is a significant fact that the wing is always located between the epimeron and the tergum, which he thinks is the typical situation of the spiracle. The thoracic spiracles of adult insects, however, almost invariably occur in the intersegmental membrane, or occupy an intersegmental position so that Palmen's premises and conclusions in these matters are wholly incorrect.

Plateau's conception of the wing as an hypertrophied spiracle which has become widened and flattened to form the wing lamellæ, while the "supporting rods" (tænidia?) of the trachea become enlarged to form the wing nervures, is entirely fanciful, as is his idea that the halteres of the Diptera (which he rightly identifies as modified wings) are modified spiracles. Indeed, the only semblance of proof offered by him in support of his theory, is in the observations of Weismann (1866) which he cites, pointing out that Weismann's investigations concerning the development of *Corethra* would indicate that in this insect, the dorsal prothoracic cell-islands, or "imaginal disks," form the pupal spiracles, while those of the mesothorax form the wings, and those of the metathorax form the halteres. It is by

no means certain, however, that the prothoracic islands are homodynamous with the wing disks, and the proof offered by Plateau in support of his theory seems rather inadequate.

The observations of Pratt (1899), Tower (1903) and Verson (1890-1894) might, in some measure, be taken as upholding Plateau's theory that the wings are modified spiracles. Thus Tower (1903) states that when the mesothoracic spiracle migrates forward, "the spiracle alone migrates, and the thickened area of the hypodermis remains and probably becomes the fundament of the elytron." Powell (1905), however, combats the idea that the wings develop from the discs of the degenerated spiracles of the meso- and metathorax, and, in opposing Tower's statements, asserts that in some Coleoptera the spiracles have not migrated forward, and that the wing primordia (or fundamentals) arise distinctly above or below the positions occupied by the thoracic and abdominal spiracles. He therefore concludes that Tower's conclusions in this matter are incorrect, and the fact that his investigations were made in the same order of insects (Coleoptera) studied by Tower, should have considerable weight, especially since he sought to verify Tower's work in carrying out his own investigations.

Many investigators, even in modern times, have advocated the derivation of wings from tracheal gills. Owen (1848) supports the idea promulgated by Oaken (1831) that the wings are modified gills, such as are born on the tergal region of Annelids, and Ganin (1869) ascribes a respiratory function to the wings.

Carus (1839) states that in the "immature *Agrion puella*, the blood circulates in the forming wings exactly as in gill plates, and it would be difficult to find a more perfect demonstration of the fact that the wing is a modified gill" (*teste* Plateau, 1871).

Enderlein (1902) suggests that since the ancient pterygote insects lived in an atmosphere of great humidity, they may have used their wings as a sort of "gill" (since the wings are supplied with tracheal branches in the early stages of development), but does not enter into the controversy as to whether the wings were derived from the tracheal gills of Ephemeropterid nymphs, or not.

Gegenbauer (1870-1878), who regards the wings of insects as derived from the dorsal gills of their Annelidan ancestors, has done so much to clearly formulate the theory that the wings are modified

tracheal gills (such as those found on the abdomen of immature Ephemeroidea), that his name is usually associated with the theory ascribing the origin of the wings to the tracheal gills. Many subsequent investigators have accepted his views, wholly or in part, and have endeavored, with varying success, to overcome the objections to the theory in question. Among the supporters of the theory of the tracheal-gill origin of the wings of insects may be mentioned Landois (1871), Lubbock, (1873), Graber (1877), Palmen (1877), Hofmann (1879), Adolph (1879-1881), Brauer (1885), Cholodkovsky (1886), Redtenbacher (1886), Lang (1888), Verson (1890), Simroth (1891), Pratt (1899), Osborn (1905), Woodworth (1906), J. A. Thomson, and many others. Cholodkovsky (1886) also thinks that the wings are homologous with the prothoracic patagia<sup>1</sup> (not the tegulae) of the Lepidoptera, and Walton (1901) even goes so far as to regard the tegulae as wings in the process of formation!

Some investigators, perceiving the difficulties inherent in the attempt to derive the wings from tracheal gills, have attempted to avoid the difficulty by suggesting that the wings may not have been derived from gills, but gills may themselves have been derived from wings, or both wings and gills may have had a similar origin. Thus, Redtenbacher (1886) thinks that wings and tracheal gills are homodynamous, but "it is questionable whether the wings were derived from tracheal gills, since the converse may be true; and that wings may have become metamorphosed into gills, is not beyond the realm of possibility." He likewise compares both wings and gills to the pronotal expansion of Mantids, etc.

Lang (1888) was impressed with the fact that aerial respiration is clearly the primitive one in insects, and in order to derive the wings from tracheal gills, suggested that insects, at first terrestrial, became adapted for aquatic life; respiratory folds of the integument into which tracheae penetrate, being modified into gills, and these eventually becoming metamorphosed into wings—which thus are ultimately derived from integumental folds.

Grassi concludes that wings and gills may be homodynamous (*i. e.*,

<sup>1</sup> It is perhaps unnecessary to mention, in this connection, that the elytra of Coleoptera, etc., are not homologous with the patagia or tegulae, as some writers have erroneously stated is the case. Their structure and development clearly shows that they are modified fore wings and nothing else.

of the same series), but that wings are not derived from gills. He goes on to show that in certain Lepismatidæ there occur tergal folds (well supplied with tracheæ) which serve to protect the sides of the thorax and the base of the legs. These lateral tergal expansions he compares to the lateral folds of the carapace of Crustacea (*teste* Henneguy, 1904), and suggests that they became transformed into gills in those insects which became adapted for aquatic life, while they were metamorphosed into wings in the aërial forms.

Graber (1875) suggests that the wings of insects may have arisen in two ways. Thus in the terrestrial forms (*e. g.*, Termites) they may have been derived from tergal outgrowths, while in the aquatic forms (*e. g.*, Ephemeroidea) they arise as metamorphosed tracheal gills. He also clearly points out that the lateral expansions of the Locustid pronotum are homodynamous with the wings.

The foregoing views lead up to the discussion of those theories in which it is maintained that the wings arose as lateral expansions of, or near, the tergal region, and were not necessarily connected with a respiratory function primarily. Since they are always borne "alongside" of the nota, or tergal plates, for the sake of convenience, in the following discussions, I would refer to these lateral folds as the "*paranota*," regardless of whether they are entirely tergal in origin, or entirely pleural, or a combination of both. The theories dealing with this origin of the wings may therefore be referred to as the paranotal theories.

Among the earliest of the theories advocating a paranotal origin of the wings may be mentioned the views of Mueller, 1875. From his studies on the development of the wings of the Termite *Calotermes*, Mueller concluded that the wings did not arise from tracheal gills, but from lateral tergal expansions (*paranota*) similar to those found in the pronotum of *Calotermes*, which greatly resemble the wings in their mode of development. Pancritius (1884) also supports this view, and likewise lays stress upon the fact that the tracheæ enter the forming wings at a comparatively late stage in certain immature insects—as Mueller had pointed out was the case in *Calotermes*. Bugnion (1911) has also called attention to the prothoracic structures of *Coptotermes flavus*, "whose larvæ bear rudiments of prothoracic wings."

The investigations of Mueller (1875) on the development of the



Termites' wings, and of Woodward (1876), who pointed out that the aliform lateral expansions (paranota) of the pronotum in the fossil insect *Lithomantis carbonaria* are homodynamous with the wings, have furnished a firm foundation for the paranotal theory of the origin of the wings, and this view has been accepted wholly, or in part, by many subsequent investigators, among whom may be mentioned Huxley (1877), Haase (1886), Korschelt and Heider (1891), Zacharias (1892), Krueger (1898), Packard (1898), Comstock and Needham (1899), Powell (1904-1905), Duerken (1907), Lameere (1900-1908), Handlirsch (1906-1908), McMurrich, and others.

From the foregoing discussion, it is evident that the two theories which have received the most widespread acceptance, are the tracheal gill theory and the paranotal theory of the origin of the wings—and opinion seems to be pretty evenly divided between the two. The evidence brought forward in support of the other theories seems insufficient to warrant their acceptance, nor does it appeal as strongly as the two mentioned above do, to our ideas of the factors and method of evolution; so that it is preferable to suspend judgment upon the other theories (until more evidence has been accumulated) and to select as a "working basis" one of the two theories which appear to be in accord with the greatest number of known facts—in other words, we must (for the time being, at least) choose between the tracheal-gill theory and the paranotal theory of the origin of the wings of insects.

Unfortunately, all of the evidence bearing upon the subject is not accessible to me at this time; but such of the arguments as were available have been brought together in the following comparison of the two theories. In addition, such evidence as has suggested itself as having a bearing upon the subject under discussion, has been added to strengthen either side of the question impartially; and I feel convinced that sufficient evidence is at hand, to make an unbiased decision in favor of one theory or the other.

It must be admitted that the tracheal gill theory is a fascinatingly clever one, and if the premises of its arguments be granted as correct, the logic of its appeal is almost irresistible; but if the rival theory is fully in accord with the same facts (or even more of the known facts) which have been cited as evidence of the tracheal gill theory, and is not open to the same objections as might be raised against this

theory, we have no alternative other than to choose the more probable and acceptable theory.

Some of the arguments which may be advanced in favor of the tracheal gill theory of the origin of the wings of insects may be summarized as follows:

1. Wings cannot have suddenly sprung into being (like Minerva from the brain of Jove!) fully formed and immediately functional, but the process of their development must have been a gradual one; and in their early stages they could not have been of use as flying organs, but must have served some other purpose while becoming wing-like. In other words, the locomotor function must have gradually become predominant in structures having a prior function or significance.

2. Wings, in their immature stages, contain tracheæ, and this indicates that their prior purpose was respiratory—either in an intensely humid atmosphere, or in water.

3. If the successive segments of an insect's body are mutually homologous, we should expect to find structures which are homodynamous (*i. e.*, of the same developmental series) with the wings, on the other segments. Superficially, at least, the tracheal gills on the abdominal segments of certain immature Ephemeroidea appear to fulfil this requirement.

4. The tracheal supply of the tracheal gills appears to be somewhat similar to that of the immature wings (see Plate I, Fig. 4).

5. The tracheal gills of some Ephemeroidea nymphs are remarkably similar, in outline, to the wings of certain insects (see Plate I, Fig. 2).

6. The gills may be bordered with hairs similar to those of certain wings, and are even stiffened by structures strongly suggestive of nervures (Plate I, Fig. 2).

7. The gill plates of immature Ephemeroidea are capable of very rapid movements for setting up currents to keep the water in contact with the respiratory surfaces pure.

8. Through their movements, the gill plates have become articulated to the tergum, after a fashion, thus "paving the way" for the articulation of the wing-like structures to be developed from them.

9. The muscles involved in the movements of the gill plates could eventually become modified to form muscles of flight.

10. Certain gill plates of immature Ephemeroidea (*c. g.*, *Tricorythus*), and especially the anterior ones, or those nearest the thorax, may become very large, and serve as coverings for the gills, thus indicating an inherent tendency to increase in size on the part of the anterior gill plates, and making it readily conceivable that similar structures might increase to the size of wings.

11. If the gills grew large enough or powerful enough, and became properly adapted, it is conceivable that such organs, already capable of rapid movement, might develop into structures capable of propelling the insect through the water, and would eventually enable it to glide over the surface of the water.

12. As the locomotor function gradually predominated, it did so at the expense of the respiratory function, which became of less and less importance until the wings became practically entirely locomotor and those which were situated on the thoracic region, being the nearest to the center of gravity, were the ones eventually retained when aerial locomotion was achieved.

13. Some insects (*c. g.*, the aquatic Hymenoptera described by Lubbock, 1863) even now use their wings for propulsion through the water, and thus make it more readily comprehensible that wings might have originated from structures formerly adapted for propulsion through the water (such as the modified wing-gills might have been).

14. It is a very significant fact that the Plecoptera, which are in some ways the most primitive of winged insects now living, are water dwellers in their immature stages. The Ephemeroidea and Odonata which are also very primitive in many respects are likewise water dwellers in their immature condition. If ontogeny is a recapitulation of phylogeny, this might be taken as an indication that winged insects at one time passed through a water-dwelling stage.

15. The Neuroptera, which occupy a position intermediate between the very primitive and the very highly specialized winged insects, and even some of the very highly specialized insects, such as the Diptera, Coleoptera, etc., have aquatic larvæ, so that the tendency toward an adaptation to aquatic life is still quite widespread, cropping out as it does in the most diverse forms, and might have been inherent in the Pterygote stem.

16. Some members of groups which are very primitive, such as

the Blattide (Shelford, 1907), Phasmids (Murray, 1866, Wood-Mason, 1878, and denied by Gahan, 1912), etc., have retained the power of adaptation to aquatic life even in the adult stages.

17. Certain very ancient fossil Pterygote insects, which must be considered as near the ancestors of modern winged forms, have retained even in the adult condition, what appear to be abdominal gills homodynamous with the wings (see Plate II, Figs. 8 and 12). If these are really gills, we must consider that the wings are homodynamous with, and hence homologous with, the tracheal gills.

18. Even present-day Apterygota, which are considered by many as having departed but little from the condition of the forms preceding winged insects, show a marked tendency to select damp locations as their dwelling places (*e. g.*, under stones, places near the coast, etc.), and we can thus more readily understand that there was a tendency on the part of the precursors of winged insects, to select damp locations to live in, and eventually become adapted for aquatic life.

19. Embryology and the ontogenetic development of certain Ephemerids would indicate that aërial respiration is the more ancient one, but this does not preclude the possibility that although originally air-breathing, the ancestors of winged insects became *temporarily* adapted for aquatic life (in accordance with the widespread tendency) at one stage of this development (*i. e.*, before wings arose) and afterward became aërial breathers once more.

20. It is also possible to regard wings and gills as homologous structures, without maintaining that wings were developed from gills, or gills from wings; but both may have been derived from a common origin (*e. g.*, lateral folds of the body wall, into which tracheæ later penetrated).

21. As a final point, it has been brought out that it is very difficult to see how rigid expansions of the tergal region could have acquired an articulation with the tergum (or how they could have become capable of the movements of flight) in the air alone. On the other hand, since the tracheal gills already have an articulation with the tergal region, after a fashion, and are capable of rapid movements, the difficulty of acquiring the ability to perform the movements of flight would not be as insurmountable.

It is thus very evident that the arguments in favor of the tracheal-

gill origin of the wings are apparently very forceful, and it must be admitted that they exert a subtly fascinating appeal; but there are certain seemingly insurmountable objections to the acceptance of the tracheal-gill hypothesis, as will be pointed out in the following discussion of the paranotal theory. The paranotal theory, on the other hand, is not open to these objections, and is even more in accord with the observed facts, as will be shown later, so that for the present, at least, it is the more probable and acceptable theory.

The principal points in favor of the paranotal origin of the wings, and the objections to the tracheal-gill theory may be briefly reviewed as follows:

1. Since the successive segments of an insect's body are mutually homologous, we should expect to find structures homologous with the wings, on the other segments. Now in order to derive the wings from such structures, it must be shown that they are homologous with them, and in order to be homologous with the wings, these structures must be homodynamous (*i. e.*, of the same developmental series) with the wings—otherwise, it would be impossible to derive the wings from them. If then, it can be shown that the wings are not homodynamous with the tracheal gills, the theory that the wings are modified tracheal gills immediately becomes untenable.

In his embryological studies of Ephemeroidea, Sialids, etc., Heymons (1896) has clearly demonstrated that wings do not arise similarly to tracheal gills, and that the tracheal gills are not homodynamous with the wings—and these investigations alone, are sufficient to entirely refute the tracheal gill theory of the origin of the wings! Furthermore, Heymon's conclusions based upon the embryology of the Ephemeroidea, etc., are fully borne out by the work of Duerken (1907) who has shown that the structure and musculature of the gills of Ephemeroidea are not comparable to those of the wings, and Boerner's (1909) studies on the tracheal gills of Ephemeroidea have shown that the gills are not homodynamous with the wings. Indeed, as Fernald (1890) and others have pointed out, the gills may occur in various localities, and even between the wings, so that under these conditions, it is not surprising that embryological and anatomical investigations have demonstrated that the gills are not homodynamous with the wings.

2. If it could be shown that, in certain immature Ephemeroidea

which have both gills and paranotal structures, the paranota are homodynamous with the wings, while the tracheal gills are not, this would be a heavy blow to the tracheal gill theory, and a correspondingly weighty argument in favor of the paranotal theory. Fortunately, we have just such an insect, in the "larva" of the singular New Zealand Ephemeropterid *Oniscigaster wakefieldi* described by MacLachlan (1876). In the immature stages of this insect, the paranota are borne along the *sides* of the tergal region (see Plate II, Fig. 15) in the position characteristic of the wing location, while the tracheal gills are borne high up on the dorsal region, and are not of the same series as the wings. The abdominal paranota and the wings are both retained in the adult condition, while the gills are lost when the insect becomes mature, showing that they are merely temporary adaptational structures, unlike the more lasting paranota.

3. The paranota are borne along side of the tergal region in the location characteristic of the wings, while the tracheal gills are attached in a very different position, thus indicating that they are not homologous with the wings. One has but to glance at Figs. 1, 6 and 7 of Plate I, or at Figs. 8 and 12 of Plate II, to see that the wings are always attached along the lateral margin of the principal tergal plate, and the paranota (*p* of Figs. 9, 12, 14, 15, etc.) are attached to the tergal region in exactly the same location; while the tracheal gills are attached either to the posterior portion of the tergal region (as in Fig. 4, Plate I) or to the dorsal region of the tergum (as in Fig. 15 of Plate II), or occupy positions unlike that of the wings!

4. The posterior margin of the principal tergal plate is always continued in the posterior margin of the wing as the so-called spring vein, ligament or axillary cord (Figs. 4, 6, and 7 of Plate I). The posterior margin of the tergum is continued in the posterior margin of the paranota (Figs. 9, 14, 15, etc., of Plate II) while the posterior margin of the tergum is not continued in the tracheal gills (Figs. 4 and 15). The inference is obvious!

5. In *Stenodictya* (Plate II, Fig. 8), *Corydaloides* (Fig. 12) and other fossil insects, there occur lateral expanded structures on either side of certain of the abdominal terga, which are homodynamous with the wings and the prothoracic paranota. Certain palæontologists have erroneously maintained that these abdominal structures are gills, and since these structures are homodynamous with the

wings, it has been claimed that this would prove that the wings are modified gills.

The structures in question, however, are not gills at all, since, as we have seen, the gills are never borne along the lateral width of the abdominal terga (as the structures in question are borne), but are attached by a narrow constricted region to the tergum, at different locations (see Fig. 4, Plate I, and Fig. 15, Plate II). The paranota on the other hand, are always attached along the lateral width of the tergal plate (as the wings are also attached) in exactly the same manner as these fossil structures! The adult of *Oniscigaster* would have shown this much better, but Fig. 15 (Plate II) depicting the condition of the immature *Oniscigaster*, if compared with *Stenodictya* (Fig. 8) will very clearly demonstrate that the lateral abdominal appendages of the fossil insect are paranota, not gills; and if we compare the abdominal paranota of the Phasmid (Figs. 11 and 14, Plate II) with the abdominal structure of *Corydaloides* (Plate II, Fig. 12), it is at once apparent that the abdominal structures of the fossil insect are not gills, but are paranota very like those of the Phasmid, and are even bordered by a similar fringe. It is evident, therefore, that the lateral abdominal appendages of these fossil insects (which are homodynamous with the wings and prothoracic paranota) are not gills, but are paranota! Since they are homodynamous with the wings, this is a clear proof of the paranotal origin of wings of insects.

6. Comstock & Needham (1898-1899), Packard (1898), Handlirsch (1906-1908) and others have pointed out that the tracheation of the wings differs from that of the tracheal gills, and this, although not in itself a strong argument against the origin of the wings from gills, is nevertheless a point in favor of those who would derive the wings from some other source, especially when taken into consideration with the other objections to the tracheal gill theory.

7. In the ontogenetic development of the wings, these arise as projections into which the tracheæ subsequently penetrate, and in many immature insects the developing wings are not penetrated by the tracheæ until comparatively late in their development, so that if the ontogenetic sequence has any meaning, the wings must first have arisen as projections (paranota) not having a respiratory function, but later the tracheæ grew out into them. It is possible to avoid this

objection by saying that both wings and gills may have been derived from a common source (*e. g.*, integumental folds) which was not originally respiratory; but this savors too strongly of an attempt to avoid the issue, and, as been shown in point (1), the wings and gills are not homodynamous—so cannot have originated in a common source!

8. Comstock & Needham (1898-1899) have shown that the wing nervures of all insects are reducible to one common "ground-plan," and a glance at Figs. 1, 6, and 7, of Plate I, will show that the little plates (ossicles) by means of which the wings are articulated to the tergum are practically identical in all. The wings are always borne in the same location, alongside the principal tergal plate, and the posterior margin of this plate is always continued in the posterior margin of the wings as the so-called spring vein, ligament, or axillary cord as may be seen from the preceding figures. From these, and other facts, it is logical to suppose that the wings of all insects originated in a common source (*i. e.*, did not have separate origins), and probably arose in a common group of ancestral insects. It is not possible therefore to suppose that the wings of some insects arose from paranota, while others arose from tracheal gills and other structures, since the great uniformity of structure and location, etc., would make such a supposition extend too far beyond the laws of probability! On this account, we are justified in rejecting the suggestion that the wings of aquatic insects arose from tracheal gills, while those of terrestrial forms arose from paranota, or similar structures, as will be discussed in the next paragraph.

9. Since the wings of all insects had a common origin, if all wings are to be derived from tracheal gills, all winged insects are all descended from ancestors which breathed by means of tracheal gills, and should show traces of such an ancestry in their individual development. The very opposite is the case, however, for even in those insects which are supposed to best illustrate the transition from gills to wings (*i. e.*, the Ephemeroidea), the primordia of the "open respiratory system" (for aerial respiration) are laid down at an early stage of embryological development, long preceding the development of the "closed respiratory system," for aquatic respiration. Even in the water-dwelling immature Ephemeroidea, the spiracles of the open system may become temporarily open to the exterior, at the time of molting, but quickly become closed again, since the insect is not yet



ready for aërial respiration; and the investigations of Palmen (1877) have clearly shown that the open respiratory system is the more ancient, and therefore the original one, while the closed one for aquatic respiration is evidently the product of a process of adaptation to aquatic life which was subsequently acquired.

Since the open respiratory system for aërial respiration is clearly the more ancient, and hence the original one even in aquatic forms, it is evident that all insects are descended from terrestrial forms, which could not have borne tracheal gills; and we can therefore state with conviction that the wings of modern insects could not have been derived from tracheal gills. The adherents of the tracheal gill theory, however, would attempt to avoid this difficulty by suggesting that although the ancestors of all insects were originally air breathers, the ancestors of the winged forms became *temporarily* aquatic, and thus acquired the gills which were to develop into wings when they became air breathers once more! This argument is clearly an attempt to again avoid the issue, but is also unavailing! If the ancestors of winged insects were all gill breathers at one time (which must have been rather recent), why do no fossil forms show traces of such "wing-gills," and why do we have no recent forms which have retained structures suggestive of this common origin of the wings? The Ephemeroidea cannot be taken as examples of this, since it has been shown (point (1)) that the wings of Ephemeroidea are not homologous with the gills, and the ontogenetic development of no other winged insect offers any hint of such a common origin for the wings in gill-like structures!

10. Palæontology shows that the earliest fossil insects had wings, yet these have retained no series of abdominal gills homodynamous with the wings, the only abdominal structures which are homodynamous with the wings being paranota, as has already been pointed out (see point (5)).

11. The great mass of lower pterygote insects are not aquatic, but are terrestrial, whereas if all pterygote insects passed through an aquatic stage, we would expect that the great majority of the lower winged forms would still be aquatic, at least in the immature stages. On the other hand, numerous lower pterygote insects have retained paranota in the prothoracic region, at least, while tracheal gills occupying the typical wing location are wanting in all of them.

12. None of the apterygote forms, which have departed but little from the ancestral condition (and the Lepismids may be taken as forms "annectent" between the Apterygota and lower Pterygota), show indications of a tendency to develop tracheal gills, while many of them bear paranotal expansions of the pronotum and other tergal projections (see Fig. 16, Plate II).

13. Unlike the tracheal gills, the paranota have been retained in the most diverse insects, being preserved in the prothorax of certain Mantids (Fig. 9, Plate II), Heteroptera (Fig. 10, Plate II), Coleoptera (Fig. 13, Plate II), Lepismids (Fig. 16) etc., as well as in the abdominal region in certain Phasmids (Figs. 11 and 14, Plate II), etc., and the paranota also occur on many of the segments in numerous "larval" forms (*e. g.*, in immature Plecoptera and Ephemeroptera, as shown in Figs. 15 and 18 of Plate II) and are specially well developed in certain Coleopterous larvæ such as those of the Sylphidæ, of *Psephenus lecontei*, and many others. This would indicate an *inherent tendency* in the insect stem, toward the formation of lateral integumental expansions, or paranota, and the fossil forms also exhibit this tendency (see Figs. 8 and 12, of Plate II).

14. Unlike the tracheal gills, the tendency toward the formation of paranotal expansions is apparently inherent in the Arthropod stem—at least in those Arthropods whose lines of development parallel that of the Insecta—and finds opportunity for expression in the most diverse forms. We thus find paranota developing in the Diplopods (Fig. 17, Plate II), in the Crustacea (Fig. 19, Plate II), in the Trilobites (Fig. 20, Plate II) and many other groups, and even in Arthropods more remotely removed from the Insectan stem, this inherent tendency may find opportunity for expression—although in certain of these more remote forms, I am not certain that we are dealing with structures strictly homologous with the paranota. Thus Berlese (1906–1909) has figured a series of Acarina (Oribatidæ) in which can be traced the gradual development of lateral "pteriform" expansions of the dorsal region, which are small in *Oribatula plantivaga* and *caliptera*, but become greatly developed in *Oribates latipes*, while in *Oribates alatus* these "pteriform" appendages actually become articulated with the tergal region. Furthermore, they do not have to pass through a tracheal gill stage in order to develop an articulation with the tergite—as Woodworth would claim that integumentary ex-

pansions which are eventually to become wings, must do, in order to develop an articulation with the tergum! I have not examined these "pteriform" expansions of the Acarina, however, and would not attempt to state whether or no they are homologous with the wings of insects.

15. The fact that paranotal expansions can become large enough to act somewhat after the fashion of a parachute, or gliding planes, to break the fall of the insect, is shown by the pronotal development of the Mantid *Charadodis* (Plate II, Fig. 9). The dried specimen will "sail" for a considerable distance, if dropped from a height, and I imagine that the living insect could do the same. Tracheal gills of such a size are unknown.

16. In order to function as a gliding plane, the paranotal expansions should be developed in insects which have a tendency to leap into the air, otherwise the expansions would not have much of an opportunity of functioning, unless the insect were to drop from a height.

Since the Mantids such as *Rhombodera*, *Charadodis* (Fig. 9, Plate II), etc., have developed such large pronotal paranota, I have asked Mr. A. N. Caudell (to whom I am indebted for the determination of the Mantid and Phasmid depicted in Figs. 9, 11, and 14, Plate II) whether the Mantids exhibit any tendency to leap, and would quote the following from his reply. "I have seen our native species leap a couple of inches, and *Yersinia*, a western species, can leap half a foot. *Ameles*, from Portugal, is reported by Wood-Mason as being able to leap nearly a foot straight upwards. In all cases it is the nymphs that leap and in some cases the hind femora are distinctly enlarged as in the saltatorial groups."

It is thus evident that forms having large paranota may also exhibit a tendency to leap, but I have been unable to find an instance of nymphal Ephemeroidea (or forms with flat tracheal gills) exhibiting a tendency to leap.

17. It might be further remarked that the leaping tendency "crops out" in the most diverse forms, such as the Apterygota (*e. g.*, *Machilis*, etc.), the Psyllids, Flea-beetles, etc., and may possibly indicate an inherent tendency in the insect stem, which finds opportunity for expression in certain forms, and would of course be especially useful in those insects which have developed large paranota.

18. The leaping habit appears in the most diverse Arthropods (*e. g.*, Arachnids, Talitridæ and other Crustacea, etc.) and may indicate a stem tendency in a group which also exhibits the tendency to the formation of paranotal expansions.

19. It is possible for certain forms closely allied to the Insecta (such as the Crustacea) to develop the power of gliding through the air for several rods, thus making it more readily comprehensible that insects could have developed the power of a gliding "flight" in a somewhat similar fashion.

Worcester (1914) observed the "flight" of such a Crustacean, while boating near the coast of Palavan, at the edge of the shoal off East Island (in the Philippines), and describes the creature as follows: "It looked more like a crayfish or shrimp with one or two pairs of much flattened legs directed forward and others curving backward, the legs and the lobes of the tail making the supporting planes . . . it was unquestionably a very transparent crustacean from fifteen to twenty centimeters in length . . . and there remains no doubt of the existence in the Philippines of a marine crustacean from fifteen to twenty-five centimeters in length, which has the power of rising rapidly from the water and flying after the fashion of a flying fish, for several rods." The specimens observed invariably rose against the wind.

We know of no parallel case in which tracheal gills have been used as gliding organs!

20. If ontogeny in a measure recapitulates phylogeny, the forming wings of the lower pterygote insects should pass through a paranotal stage, if the wings were derived from paranota—and conversely, if they were derived from tracheal gills, they should pass through a stage comparable to tracheal gills. If we observe the forming wings of the most primitive winged insects, such as the Plecoptera (Fig. 18, Plate II) or the Blattids and Mantids (Fig. 9, Plate II) it is clearly evident that the upper surface, at least, of the wings arise as paranotal expansions of the tergum, rather than as tracheal gills! Furthermore, since the wings of all insects must have had a common origin (as was brought out in the previous discussions) the wings of insects with a complete metamorphosis should show traces of a tergal origin, and this Heymons, 1896, has shown to be the case in the beetle *Tenebrio*.

21. As to the argument that the wings could not have acquired an articulation with the tergal region, save through first becoming a tracheal gill (the tracheal gills have already acquired such an articulation), I fail to see the logic of such reasoning.

If an expansion of the integument can acquire an articulation with the body when it develops into a tracheal gill in the water, why can not a similar expansion acquire an articulation with the tergum when it becomes a wing in the air? It is surely no harder to conceive of a rigid outgrowth becoming an articulated appendage in the air, than to conceive of a similar rigid outgrowth becoming an articulated appendage in the water! When the forming wing of a Blattid develops from an immovable outgrowth near the tergal region, it does not first become a gill before acquiring an articulation with the tergum, and if this can take place during the ontogenetic development of the insect, why can it not occur in the phylogenetic development of the race?

Furthermore, in the series of Acarina, described in point 14, these forms have acquired appendages articulated with the dorsal region, without having these appendages pass through a tracheal gill stage in either ontogenetic or phylogenetic development, and if such an articulation can occur in the air, in such forms, why can it not occur in the wings also, without their first passing through a tracheal gill stage?

On page 242 of his "Cours d'Entomologie," Latreille, 1831, has described a Coleopteron *Aerocinus longimanus*, whose prothorax bears articulated lateral processes (*teste* Cholodkowsky, 1886). If these can become articulated to the prothorax without first passing through a tracheal gill stage, why can the wings not do the same? To demand that the wings must pass through a tracheal gill stage in order to become articulated to the tergum, is asking far more than the facts would warrant, and in the light of the foregoing instances, this objection to the origin of the wings from paranota, is not valid.

In a footnote to page 360, Walton, 1901, makes the following statement. "The prothoracic appendages of certain fossil insects (*Homoioptera woodwardi*, *Stenodicta lobata*, *Lithomantis goldenbergi*, *carbonaria*, etc.) so excellently figured by Brongniard (1894) cannot be homologized with the expanded margin of the prothorax in existing Mantidæ, as Woodward, 1879, suggested. Brongniard,

1890, has already pointed this out." Walton gives no reason for this statement, and Brongniart's work is not now accessible to me, so that I do not know what evidence he has adduced in support of this contention. If one will compare Fig. 8 (Plate II) of *Stenodictya* with that of the Mantid, *Charadodis*, depicted in Fig. 9, however, it will be apparent that the paranota of the Mantid's pronotum occupy exactly the same location as the prothoracic paranota of the fossil insect (*Stenodictya*), and why they are not to be considered homologous is not apparent. It is not evident that the paranota of the fossil insect's prothorax are articulated or movable, and even though they were, the case of the beetle *Acrocinus* cited above, would indicate that pronotal paranota may be articulated even in existing forms.

In reply to the argument that the precursors of wings must have served some useful purpose while developing, one might state that when we are dealing with an inherent stem tendency (as the development of paranotal projections seems to be) it is unnecessary to postulate that the products of such a tendency must serve some useful purpose—so long as the result is not detrimental to the organism, whereupon natural selection would operate to check further development along such lines. It is not beyond the realm of possibility, however, that the paranota may have served a useful purpose (before becoming adapted for gliding flight) in that they may have served to shield the flanks and basal portions of the legs, as Grassi has pointed out.

It is evident from the foregoing discussions, that the objections which might be raised to the paranotal theory are not insurmountable. On the other hand, there are certain insurmountable difficulties in the way of accepting the tracheal gill theory, as were shown in points (1), etc., although these difficulties do not apply in the case of the paranotal theory. Furthermore, the paranotal theory is in full accord with all of the known facts—which is more than can be said for the tracheal gill theory!

In making a choice between two rival theories, our selection should not only be free from insurmountable objections (or should not be incompatible with any of the known facts), but should also have the positive quality of being in full accord with all of the known facts. If we apply this criterion in selecting one of these theories, the paranotal theory, being the only one which fulfils the conditions, must therefore be chosen, and has been here adopted as a provisional

working hypothesis, in the following discussion of the nature of the wings:

Despite the contentions of Landois, 1874, Ganin, 1876, and Graber, 1889, practically all embryologists have accepted the view that the wings of insects are of hypodermal origin, but whether they are tergal, or pleural (or both) in nature, is still an undecided question. In the paranota of Arthropods in general, these integumental outgrowths appear to be of a tergal nature—at least the dorsal lamella of the paranota is apparently a continuation of the surface of the tergum. So too, the upper surface of the developing wing of the Blattidæ and other primitive winged insects appears to be a direct continuation of the tergum. The view that the wings are merely lateral expansions of the tergum has been strongly combated, however, and it is necessary to appeal to the evidence afforded by embryology. The following views have been put forth by those who have studied the development of the wings.

According to Tower, 1903, Rehburg, 1886, and Palmen, 1887, the wings are pleural in origin. Mayer, 1876, also states that the wings are not purely dorsal, but are lateral outgrowths of the body wall.

Powell, 1905, states that in the Coleoptera “the wing arises on the pleurum at or near the future position of the dorso-lateral suture (*i. e.*, the suture between the tergum and pleuron) as a thickening of the body wall which in the simplest type begins as a simple projecting outward and downward of this thickening.” He also states that “wings have been derived as lateral outgrowths or folds of the hypodermis of the pleurum or tergum or both.”

Comstock and Needham, 1898-1899, state that the wings “appear at a time when the tergum and pleura are very little chitinized and are hardly more identified with one than with the other,” and that they arise “at the point where the suture between the tergum and pleura later develops.” Calvert, 1893, thinks that in the Odonata, the upper lamina of the wing is tergal, and the lower one pleural.

Marshall (1913) states that in the Trichoptera, “each wing rudiment is situated under the dorsal plate (*i. e.*, tergum) a little above its lateral margin,” and would thus indicate that the wing is tergal in origin. Later, however, “it would appear that when the wing becomes external, its position would be between the tergum and pleurum.” Packard (1898) from his observations on the develop-

ment of the Hymenoptera, and other studies, concludes that the wings "are outgrowths of the scutal region of the notum" (or tergum). He also states that "in the house fly, the wings are evidently outgrowths of the meso- and metanotum," as shown by his earlier studies of the development of these Diptera (Packard, 1874); and further remarks that "the wings in all hemimetabolous insects are outgrowths from the notum, and not from the flanks or pleurum of the thorax." The numerous embryological studies of Heymons, 1895-1899, have clearly shown that the wings are tergal structures, even in Coleoptera (*Tenebrio*, etc.), and Heymon's observations, including as they do such diverse forms, should have considerable weight, aside from his acknowledged ability as a keen observer. The view that the wings are tergal structures is supported by a great number of other investigators, among whom may be mentioned Duerken (1907), Voss (1905), Kruger (1898), Haase (1891), Simroth (1891), Cholodkowsky (1886), Pancritius (1884), Dohrn (1881), Hofmann (1879), Mueller (1875), Huxley (1877) and others.

As pointed out by the writer (Crampton, 1908-1914) and others the posterior margin of the principal tergal plate is continued in the hind border of the wing, as the so-called spring-vein, axillary cord, or ligament (see Figs. 1, 6 and 7, of Plate  $\frac{1}{r}$ ), and this fact, together with the mode of development of the wings in the Blattidæ and other primitive insects, would indicate that the wing (or at least its dorsal lamella) is tergal in nature. The wings, as we have seen, are entirely homologous in all insects, so that all have a common origin, and what is true of one, holds for all. The foregoing facts would therefore indicate that the wings of all insects are, at least in part, of a tergal nature, and the studies of Heymons (1895-1899) and others cited above would substantiate the view that the wings are tergal in origin; so that for the time being, this view may be accepted as being as probable as any; although subsequent investigation may show that the lower lamina of the wing, or its basal portion, may be pleural in nature.

The wings, then, are organs of paranotal origin, and are wholly or partially tergal in nature. In other words, they arose as paranotal expansions of the tergum, although the lower lamella of the integumentary fold forming them may be in part pleural.

As to the articulation of the wings with the body, there are three



principal fulcra, or pivots, used in the movements of flight. Two of these fulcra are dorsal, and one is ventral (with regard to the attachment of the wing). The anteriormost dorsal wing fulcrum (or suralar fulcrum) is formed by the small sclerite *sur* of Figs. 1, 6, and 7, of Plate I (compare also Figs. 4 and 6 of Diptera and Hymenoptera by Crampton, 1914 c, *i. e.*, the sclerite designated as "*sur*"; and sclerite similarly labeled in Fig. 1 by Crampton, 1914 a), which is always situated immediately behind the tegula (*tg* of the above-mentioned figures). The posterior dorsal wing fulcrum (or adanal fulcrum) is formed by a projecting region *apt* of Figs. 1, 6, and 7 (Plate I) which extends toward the anal veins (hence the name adanal), which usually articulate with it. In some forms this region may become detached to form a distinct sclerite, or plate. Between these dorsal wing fulcra, is a small plate *npt* which is present in practically all winged forms. From its location, and close connection with the notum, I think that this articulatory ossicle is a detached portion of the notum or tergum, and have therefore designated it as the notopterales (the term pteralia having been applied to the alar ossicles in general by Groeschel, 1911). The other dorsal ossicles, are, for the most part, detached portions of the basal region of the wing veins. The tegula (*tg*), however, is possibly merely a thickening of the membrane. The sclerite *m* (Figs. 6 and 7) is the only other dorsal ossicle of interest, and is mentioned because it dips downward and unites with a plate on the lower surface of the wing, as will presently be described. The various modifications of the dorsal ossicles may be readily seen by comparing Figs. 1, 6, and 7, of Plate I, with Figs. 4 and 6 of Plate VII by Crampton, 1914 c, homologous ossicles being designated by the same lettering in both instances.

The ventral fulcrum of the wing is formed by a dorsal projection of the episternum and epimeron extending upward (along the suture dividing the two pleural sclerites) as a narrow projecting region figured in Fig. 5 of Plate I. This narrow neck-like region may become detached to form a distinct plate in certain insects, but is usually more or less rigid to form the pleural fulcrum of the wing (pieuro-alar fulcrum).

Immediately in front of this fulcrum, at the base of the wing are two basalar plates (Fig. 5, *aba* and *pba*), which are sometimes in-

correctly called "paraptera." The term paraptera, however, should be applied only to the tegulæ, as was pointed out by the writer (Crampton, 1914 c); the argument that Audouin, 1824, intended that his designation "paraptere" should be applied to the plates *aba* and *pba*, being entirely unfounded. In all probability, the basalar sclerites *aba* and *pba* are detached portions of the episternum.

Just behind the pleural wing fulcrum, there may occur one or two small plates called the subalar sclerites (*sa* of Fig. 5), from their situation immediately below the wing. Whether the subalar plate is a detached portion of the epimeron or not, is questionable. In the Blattidæ, the dorsal sclerite designated as "*m*" in Fig. 7, is connected with a subalar sclerite homologous with "*sa*" of Fig. 5.

Just above the pleural alar fulcrum, is a small detached plate "*ia*" (Fig. 5), or intralar sclerite. It is connected with a dorsal sclerite homologous with that labeled "*m*" in Fig. 7. From its location, one might be led to infer that it is a detached portion of the pleural fulcrum of the wing, but the fact that it is connected with the dorsal sclerite homologous with that labeled "*m*" in Fig. 7, would indicate that this is not the case. The other wing plates are largely formed as detached portions of the bases of the wing nervures.

From the foregoing discussion, it is evident that the alar ossicles do not furnish any serviceable clues as to the nature of the wings—so far as our present knowledge of them extends, and the fact that in some insects there is a pre-alar bridge (Fig. 1, *pal*) and a post-alar bridge (Fig. 1, *poa*) extending between the tergum and pleural region, also throws no further light upon the subject. The fact that the pleuro-alar membrane (or membrane between the wing and pleural region) extends upward into the wing as a continuation of the surface of the pleural region, suggests that the basal portion of the wing, at least, might be of a pleural nature, but the evidence in the matter is insufficient to draw any trustworthy conclusions from this alone. Embryology, then furnishes the only reliable evidence at present available, and the embryological evidence, such as it is, indicates that the wings are tergal in nature.

The conclusions to be drawn from the foregoing discussion may be briefly summarized as follows.

1. The wings of all insects are homologous, and had a common origin, so that the same principles apply to the wings of insects with

complete metamorphosis, and those with incomplete metamorphosis, alike.

2. The wings of insects can not be derived from tracheal gills, since the two types of structures are not of the same developmental series (*i. e.* are not homodynamous), and are therefore not homologous.

3. The paranota, or integumental outgrowths borne alongside the tergum, or notum, are homodynamous with the wings, and wings were doubtless derived from them, since they occur in the most diverse forms (and there is an inherent tendency toward the formation of such structures in the Arthropod stem).

4. The embryological evidence would indicate that wings are of a tergal origin. We may therefore conclude that the paranota from which the wings were developed were (wholly, or in part) lateral expansions of the tergum or notum.

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## ABBREVIATIONS.

- aba* .....Anterior sclerite at base of wing (anterior basalare).
- acs* .....Upper region of episternum (anepisternum).
- apt* .....Adanal projection to anal veins (adanale).
- em* .....Epimeron.
- es* .....Episternum.
- f* .....Pleural fulcrum of wing.
- g* .....Gill plate, or branchial lamella.
- ia* .....Intra-alar sclerite (intralare).
- it* .....Tergite in intersegmental membrane (intertergite).
- m* .....Median pterale (medipterale).

<i>npt</i> .....	Notal pterale (notopterale).
<i>p</i> .....	Paranotum, or paranota.
<i>pba</i> .....	Posterior sclerite at base of wing (posterior basalare).
<i>poa</i> .....	Bridge behind wing (postalare), connecting tergal and pleural regions.
<i>pot</i> .....	Posterior tergal sclerite (postergite).
<i>pra</i> .....	Bridge in front of wing (prealare), connecting tergal and pleural regions.
<i>pri</i> .....	Anterior tergite (pretergite).
<i>psc</i> .....	Prescutum.
<i>psl</i> .....	Postscutellum.
<i>sa</i> .....	Subalar sclerite (subalare).
<i>san</i> .....	Sclerite at base of anal veins (basanale).
<i>sl</i> .....	Scutellum.
<i>sur</i> .....	Suralar sclerite (suralare).
<i>tg</i> .....	Tegula, or parapteron.

## EXPLANATION OF PLATES.

(All figures are somewhat diagrammatic.)

## PLATE I.

Fig. 1. Dorsal view of typical Plecopterous mesonotum, showing articulation of wing base.

Fig. 2. Gill plate (lamella) of *Rithogena* (Ephemeroidea) nymph, based on a figure by Woodworth, 1906.

Fig. 3. Lateral view of head, prothorax and mesothorax of immature *Coptotermes*, pronotum bearing wing-like organs described by Bugnion, 1911, on whose figures this is based. (Immature Termite.)

Fig. 4. Gill plate of immature *Heptagenia* (Ephemeroidea).

Fig. 5. Lateral view of upper portion of metathoracic pleuron and wing base of a grasshopper (*Rhomaleum*).

Fig. 6. Dorsal view of mesonotum of *Corydalis*, showing articulation of wing.

Fig. 7. Dorsal view of metanotum and wing base of *Periplaneta*.

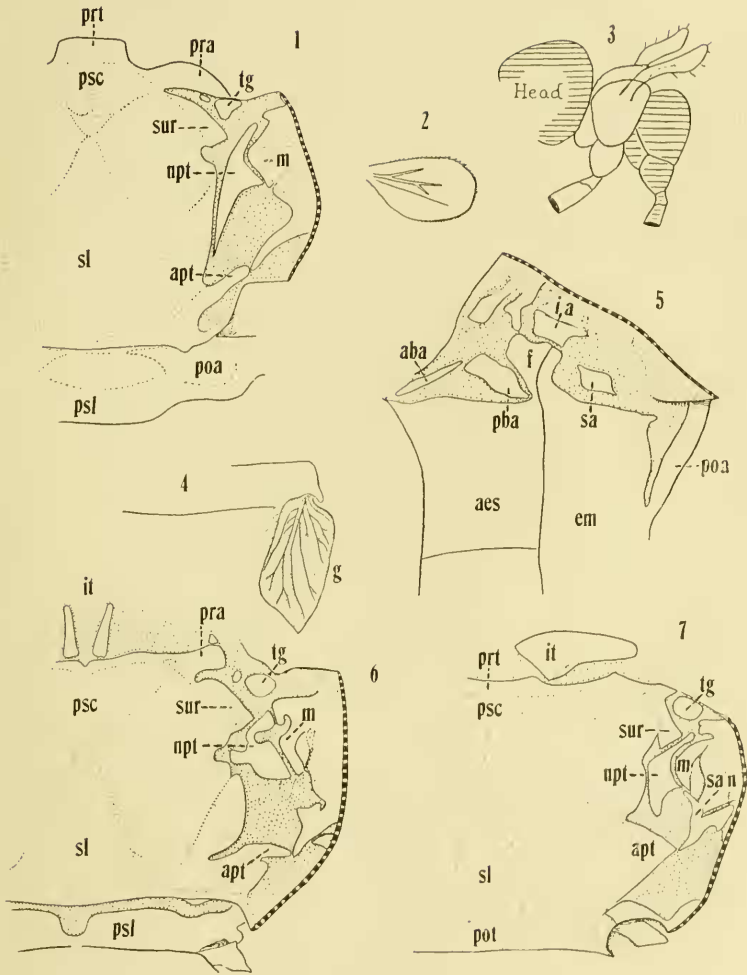
## PLATE II.

Fig. 8. Dorsal view of head, thorax and part of abdomen of the fossil insect, *Stenodictya lobata*, based on several drawings by Handlirsch, Brongniart and others. The wings are represented as though partly cut off.

Fig. 9. Dorsal view of an immature Mantid (*Charadodis*), showing developing wings and prothoracic paranota.

Fig. 10. Dorsal view of pronotum and basal portion of fore wings of a Tingitid (*Corythuca*).

Fig. 11. Lateral view of segments 6 and 7 of the abdomen of the Phasmid *Ectatosoma popa*.



Origin of Wings.